ORIGINAL ARTICLE

Dissociated Neural Representations of Pain Expressions of Different Races

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Abstract

To investigate whether coding pain expressions of own-race and other-race individuals engages overlapping or distinct neuronal populations, we recorded event-related brain potentials from Chinese and Caucasian adults when viewing an adaptor face (with pain or neutral expressions) and a target face (with only pain expression) presented in rapid succession. If distinct neuronal populations are engaged in coding pain expressions of different races, repetition suppression (RS) of neural activity to pain expressions, that is, decreased neural responses to target faces preceded by pain versus neutral adaptors, should occur when an adaptor and a target are of the same race but not when they are of different races. We found that neural responses to adaptor faces at 128–188 ms (P2) and 200–300 ms (N2) over the frontal/central areas were positively shifted by pain versus neutral expressions. Moreover, RS of neural responses to target faces in the P2/N2 windows occurred when an adaptor and a target were of the same race N2(wn-r)27.6differentofid(brtil)-278samee oidian53(ms)-271.(y)-23ae al94[(3in)-20110004489rg1278667h26

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question regarding the processing of race, namely, are there dissociated neural representations of emotional states of different races? A couple of fMRI studies have shown that perceiving own-race compared with other-race faces with happy/sad (Lee et al. 2008) or fearful (Chiao et al. 2008) expressions elicits stronger amygdala activity. ERP research that recorded neural activity to angry/happy/neutral expressions of own-race and other-race faces, however, did not find robust evidence for interactions between race and emotion cues (Kubota and Ito 2007). One line of recent research has shown consistent fMRI and ERP evidence for dissimilar neural responses to perceived pain in own-race and other-race individuals. fMRI studies reported that perceived painful stimulations applied to, or painful expressions of, own-race (versus other-race) individuals elicited stronger activity in the anterior cingulate and insula (Xu et al. 2009; Azevedo et al. 2013; Sheng et al. 2014). ERP research also discovered that perceived pain expressions of own-race (versus other-race) individuals induced greater modulations of the frontal/central activity at 128–188 ms (P2) and 200–300 ms (N2) after stimulus onset (Sheng and Han 2012; Sheng et al. 2013; Huan and Han 2014). Furthermore, in contrast to other-race encounters, perceived painful stimulations applied to own-race faces or hands also produced stronger effects on the frontal/central (Sessa et al. 2014) and sensorimotor activity (Avenanti et al. 2010).

The findings of discrepant neural responses to painful emotion of own-race and other-race individuals suggest a neural mechanism of behavioral parochial altruism during interactions with racial in-group and out-group members (Johnson et al. 2002; Drwecki et al. 2011). However, a comprehensive neurocognitive model of the processing of own-race and other-race pain remains undefined. Both early (Bruce and Young 1986) and recent (Haxby et al. 2002) models have assumed distributed cognitive and neural systems that underpin the processing of multiple features of faces. These models consist of independent modules for the processing of facial structure, person identity, facial expression, etc., but lack mechanisms designed to integrate a social feature (e.g., racial identity) and an emotional state of a face (though Haxby et al. (2002) suggested that the two types of information (stable and transient) are integrated at the level of the extended system). Similarly, the neural model of the distributed brain areas involved in race perception emphasizes how racial category membership modulates responses in different brain regions engaged in the processing of different aspects of faces [e.g., race identification and evaluation, implicit attitude, emotion, and behavior regulation (Ito and Bartholow 2009; Kubota et al. 2012)] but leaves the issue open as to how the brain differentiates between own-race and other-race facial expressions. The current work examined 2 models regarding the processing of own-race and other-race pain expressions. The first model consists of 2 neurocognitive modules with one module coding own-race pain expression and another module coding other-race pain expression. This model suggests that different neuronal populations are recruited to code painful emotional states of own-race and other-race individuals, respectively, and the neuronal population coding own-race pain responds more strongly relative to that coding other-race pain (the distinct-population hypothesis). The second model consists of 2 separate modules with 1 module coding racial identity and the other coding pain expression. The second model assumes shared modules for the processing of both own-race and other-race pain expressions, which therefore implies overlapping neuronal populations engaged in coding own-race and other-race painful emotional states (the overlapping-population hypothesis).

Although ethological observations suggest that a person experiencing pain usually sends signals to those in the vicinity in order to get social and psychological support (Schiefenhövel 1995), this may not always be the case from an evolutionary perspective (Williams 2002). In a situation of group conflict, pain expression from allies signals the demand of support and motivate approach to help. On the contrary, pain expression from an antagonist competitor may signal immediate threat and trigger avoidance or escape. Therefore, the evolutionary view favors the distinct-population hypothesis because coding pain expression of racial in-group and out-group members in separate neural assemblies may quickly connect perceived pain expression with different social significances in terms of survival. However, the previous findings of greater neural responses to perceived pain in own-race than other-race individuals (e.g., Xu et al. 2009; Sheng and Han 2012) are unable to clarify the overlapping- and distinct-population neural models.

The current work aimed to test the overlapping- and distinct-population hypotheses by using an adaptation paradigm that allows us to examine stimulus-specific repetition suppression (RS). RS refers to relative attenuation in neural responses to repeated occurrence of a stimulus (e.g., Miller et al. 1991; Henson et al. 2004). It is commonly acknowledged that RS of neural activity elicited by 2 successive stimuli indicates the engagement of an overlapping neuronal population in the processing of both stimuli (Grill-Spector et al. 2006). A paradigm to measure RS was developed in a recent ERP study that investigated whether an occipitotemporal negative component that is sensitive to facial structures, that is, the N170, engages identity coding of own-race and other-race faces (Vizioli et al. 2010). In this paradigm, 2 faces were presented in rapid succession. The first face served as an adaptor and the second face served as a target. On each trial, the adaptor and target faces were always of the same race and the RS effect was defined by decreased N170 amplitude to a target face that was preceded by an adaptor face of the same versus different person identity. The RS effect on the N170 amplitude elicited by the same-race faces was observed in both East Asian and Western Caucasian participants. However, the RS effect on the N170 amplitude linked to other-race faces occurred regardless of the face identity of target and adaptor faces, suggesting early sensitivity to identity of own-race but not of other-race faces.

To clarify whether overlapping or different neuronal populations are involved in coding pain expressions of different races, the current work modified the previous adaptation paradigm and algorithm (Vizioli et al. 2010) to estimate RS effects related to the processing of pain expressions. On each trial, a target face with pain expression was preceded by an adaptor face possessing either pain or neutral expressions (Fig. 1 and Supplementary Fig. 1). Target and adaptor faces were either of the same race or of different races. Participants were asked to perform judgments on a feature of the adaptor and target faces, that is, gender, which was irrelevant to either race or pain so as to minimize attention effects on the processing of race or pain. RS of neural activity to target faces was quantified by decreased ERP amplitudes to target faces preceded by pain versus neutral adaptors that were of the same race. Thus, the stimuli (i.e., both the target and adaptor faces) in the 2 conditions used to estimate the RS effect were identical in low-level visual features, with the only difference in the facial expressions of the adaptor faces. This algorithm allowed us to assess RS of ERP amplitudes to targets in the P2/N2 time windows, which are sensitive to pain/neutral expressions (Sheng and Han 2012; Sheng et al. 2013; Huang and Han 2014), by reducing the effect of differential

low-level visual features between target and adaptor faces to a minimum degree.

The overlapping-population hypothesis predicts that the RS effect related to pain expression should occur regardless of whether the adaptor and target faces on a trial are of the same

different in face identity. On each trial, participants were asked to judge whether the adaptor and target faces were of the same gender by pressing 1 of 2 keys. There were 8 blocks of 128 trials. An adaptor showed pain expression on half of the trials and neutral expression on others. The adaptor and target faces were of the same race (or gender) on half of the trials and of different races (or gender) on others. The stimuli were presented using the software Presentation.

To measure subjective feelings of others' pain, participants were asked to rate both the intensity of pain portrayed by each face and their own subjective feelings of the unpleasantness induced by each face on a 9-point Likert scale (1 = not at all painful or unpleasant, 9 = extremely painful or unpleasant) after the electroencephalography (EEG) recording. Participants' empathy traits were estimated using the Interpersonal Reactivity Index (IRI, Davis 1983) on a 5-point scale (0 = does not describe me well, 4 = describe me very well). We employed a race version of Implicit Association Test (IAT, Greenwald et al. 1998) to assess participants' implicit attitude toward Asian and Caucasian faces. A different set of 10 Asian and 10 Caucasian faces (half males) with neutral expressions were used in the IAT. In a block of 20 practicing trials and a block of 40 testing trials, participants were asked to categorize Asian faces/positive words with one key and Caucasian faces/negative words with another key. In another block of 20 practicing trials and a block of 40 testing trials, participants responded to Asian faces/negative words with one key and Caucasian faces/positive words with another key. The IAT was conducted using the software Inquisit. According to established algorithm (Greenwald et al. 2003), the difference in response speeds between the 2 types of blocks was calculated as an index of racial bias in attitude, namely D score. A D score larger than 0 represents that, compared with out-group faces, in-group faces are associated with positive rather than negative attitude, whereas a D score smaller than 0 represents negative rather than positive attitude toward in-group faces compared with out-group faces. Apart from implicit measurements, we also had participants rate how much they liked each face on a 9-point Likert scale (1 = not at all and 9 = extremely strong) to indicate their explicit preference for Asian and Caucasian faces.

EEG Recording and Analysis

A NeuroScan system was used for EEG recording and analysis. The EEG referenced to the average of the left and right mastoid electrodes was continuously recorded from 62 scalp electrodes. Eye blinks and vertical eye movements were monitored with electrodes located above and below the left eye. The horizontal electro-oculogram was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. The EEG was amplified (band pass 0.1–100 HZ) and digitized at a sampling rate of 250 HZ. The ERPs in each condition were averaged separately offline with an epoch beginning 200 ms before stimulus onset and continuing for 1000 ms. Trials contaminated by eye movements and muscle potentials exceeding ±50 μV at any electrode following adapter or target faces or response errors were excluded from average. This resulted in 91 ± 14 trials accepted per condition for each participant in race-based analysis and 91 ± 15 trials accepted per condition for each participant in gender-based analysis. The baseline for ERP measurements was the mean voltage of a 200-ms prestimulus interval and the latency was measured relative to the stimulus onset.

We quantified RS of neural activity to target faces by calculating decreased ERP amplitudes to target faces preceded by pain versus neutral adaptors that were of the same race. Specifically, we compared ERPs with targets in the conditions shown in Figure 1*a* versus *b*, or ERPs to targets in the conditions shown in Figure 1*c* versus *d*. Thus, the stimuli (i.e., both target and adaptor faces) in the 2 conditions used to estimate the RS effect were identical in low-level visual features except the difference in the expressions of adaptor faces between the 2 conditions. Supplementary Figure 1 illustrates the other half of the stimuli where a Chinese target face with pain expression was presented and the RS of neural activity related to target faces was similarly quantified. According to the overlapping-population hypothesis, the RS effect related to pain expression should be observed "both" when comparing ERPs with targets in Figure 1*a* versus *b* and when comparing ERPs with targets in Figure 1*c* versus *d*. However, according to the distinct-population hypothesis, the RS effect related to pain expression should be observed when comparing ERPs with targets in Figure 1*c* versus *d* but "not" when comparing ERPs with targets in Figure 1*a* versus *b*.

Mean amplitudes of the N1, P2, and N2 components were calculated at the frontal (Fz, F3, and F4) and central (Cz, C3, and C4) electrodes. Mean amplitudes of the P3 and N170 were calculated at the central/parietal (Cz, C3, C4, Pz, P3, and P4) and occipital-temporal (P7 and P8) electrodes, respectively. Repeated-measures analyses of variance (ANOVAs) were conducted on ERP amplitudes, reaction time (RT), and accuracy with Adaptor Race (own-race vs. other-race), Adaptor Expression (pain vs. neutral), Target Race (own-race vs. other-race) as within-subjects variables, and Ethnicity (Chinese vs. Caucasian participants) as a between-subjects variable. ANOVAs of the ERP amplitudes were performed on pairs of lateral electrodes (e.g., C3 and C4) with an additional within-subjects variable, that is, Hemisphere (electrodes on the left or right hemisphere). However, neither the main effect of Hemisphere nor its interaction with other factors was significant, and these were therefore not reported in the Result section. We also measured and analyzed peak latencies of ERP components, but did not find any significant results (all $F < 1$). Own-race (or other-race) refers to faces that are of the same race (or different race) with participants.

Results

Behavioral Performances

Table 1 shows the mean RTs and response accuracies during gender judgments. ANOVAs of RTs and accuracies (response accuracies were subjected to arcsine-square-root transformation before ANOVAs) did not show any significant effect ($P > 0.1$). Participants rated faces with pain expressions as more painful compared with neutral faces (6.39 ± 1.15 vs. 1.78 ± 0.94, $F_{1,30} = 422.92$, $P < 0.001$) and reported greater feelings of unpleasantness when viewing faces with pain versus neutral expressions (4.44 ± 1.96 vs. 1.77 ± 0.97, $F_{1,30} = 79.23$, $P < 0.001$). Rating scores of likability did not differ between Asian and Caucasian faces and between pain and neutral faces ($P > 0.1$). One-sample *t*-test of IAT D scores revealed that the D score was significantly larger than 0 for Caucasian participants (0.51 ± 0.28, $t_{15} = 7.29$, $P < 0.001$) but not for Chinese participants (0.18 ± 0.41, $t_{15} = 1.79$, $P = 0.094$). Independent sample *t*-test further confirmed a greater D score for Caucasian compared with Chinese participants ($t_{30} = 2.65$, $P < 0.05$). Thus, Caucasian participants showed stronger implicit positive attitude toward own-race faces, possibly due to their status of minority in China. Independent sample *t*-tests did not show any difference in IRI subscale scores between Chinese and Caucasian participants (Table 2, $P > 0.2$).

Table 1 RTs and accuracies (mean ± SD) during judgments on gender of adaptor and target faces

Observer	Adaptor expression	Asian targets		Caucasian targets	
		Asian adaptor	Caucasian adaptor	Asian adaptor	Caucasian adaptor
RT (ms)					
Chinese	Neutral	638 ± 75	638 ± 80	635 ± 78	632 ± 69
	Pain	640 ± 80	638 ± 75	638 ± 77	632 ± 76
Caucasian	Neutral	611 ± 56	614 ± 70	613 ± 63	608 ± 56
	Pain	611 ± 59	612 ± 66	611 ± 66	609 ± 64
Accuracy (%)					
Chinese	Neutral	84 ± 8.3	84 ± 6.4	86 ± 6.7	85 ± 8.2
	Pain	85 ± 6.9	85 ± 8.6	84 ± 8.4	87 ± 7.6
Caucasian	Neutral	86 ± 6.3	87 ± 6.6	87 ± 6.3	88 ± 5.1
	Pain	87 ± 7.5	88 ± 7.2	87 ± 5.8	88 ± 7.1

Table 2 Rating scores of the IRI subscales

	Fantasy	Empathic concern	Perspective taking	Personal distress
Asian	16.00 ± 4.52	19.13 ± 2.85	16.56 ± 2.53	14.31 ± 4.36
Caucasian	18.06 ± 4.58	19.94 ± 5.12	16.94 ± 4.06	12.63 ± 3.46

ERPs to Adaptor Faces

ERPs to adaptor faces were characterized by a negative wave at 84–124 ms (N1) and a positive deflection at 128–188 ms (P2) over the frontal–central area, which were followed by a negative wave at 200–300 ms (N2) over the frontal region and a long-latency positivity at 420–580 ms (P3) over the central/parietal area (Fig. 2*a*). Adaptor faces also elicited a posterior N170 at 140–200 ms over the occipitotemporal areas (Fig. 2*b*).

ANOVAs of the N1 amplitudes to adaptor faces did not show any significant effect ($P > 0.05$). ANOVAs of the P2 amplitude revealed a significant effect of Adaptor Race ($F_{1,30} > 24.47$, $P < 0.001$) and a significant interaction of Adaptor Race and Ethnicity ($F_{1,30} > 7.34$, $P < 0.05$) as other-race faces elicited larger P2 amplitudes than own-race faces in Chinese ($F_{1,15} > 30.41$, $P < 0.001$) but not in Caucasian participants ($F_{1,15} < 2.86$, $P > 0.1$). There was a significant effect of Adaptor Expression ($F_{1,30} > 30.35$, $P < 0.001$) and a significant interaction of Adaptor Race and Adaptor Expression ($F_{1,30} > 5.98$, $P < 0.05$), as the differential P2 amplitude to pain versus neutral expressions was greater for own-race faces compared with other-race faces (Fig. 2*a*). See Supplementary Table 1 for additional statistic details.

ANOVAs of the N2 amplitude to adaptor faces showed a significant effect of Adaptor Race ($F_{1,30} > 17.37$, $P < 0.001$) and a marginally significant interaction of Adaptor Race and Ethnicity ($F_{1,30} = 3.06$–4.91, $P = 0.034$–0.09), as other-race versus own-race faces reduced the N2 amplitude in Chinese ($F_{1,15} > 19.18$, $P < 0.001$) but not in Caucasian participants ($F_{1,15} < 4.46$, $P > 0.05$). There was a significant main effect of Adaptor Expression ($F_{1,30} > 32.13$, $P < 0.001$) and a significant interaction of Adaptor Race and Adaptor Expression ($F_{1,30} > 4.85$, $P < 0.05$), suggesting greater differential N2 amplitude to pain versus neutral expressions for own-race faces compared with other-race faces. Thus, the modulations of differential neural responses in the P2/N2 time windows to pain versus neutral expressions due to racial relationship between observers and perceived faces replicate our previous findings (Sheng and Han 2012; Sheng et al. 2013). See Supplementary Table 2 for additional statistic details.

The P3 tended to be of larger amplitude to other-race than own-race faces, but this effect did not reach significance ($F_{1,30} < 3.91$, $P > 0.05$). ANOVAs of the N170 amplitudes showed a significant main effect of Adaptor Race ($F_{1,30} = 14.60$, $P < 0.001$) and a significant interaction of Adaptor Race and Ethnicity ($F_{1,30} = 17.06$, $P < 0.001$), as own-race versus other-race faces elicited larger N170 amplitude in Chinese ($F_{1,15} = 22.89$, $P < 0.001$) but not in Caucasian participants ($F_{1,15} < 1$, $P > 0.7$, Figure 2*b*). Neither the effect of Target Race nor its interaction with any other factor (because the onset of a target face fell in the P3 time window of the preceding adaptor face, the ERPs to target faces might produce effects on ERPs to adaptor faces even though there was a jitter between an adaptor and a target. This is why we included the "target race" as a variable for the ANOVA of ERPs to adaptor faces to examine potential influences of target-related ERPs on adaptor-related ERPs) was significant ($F_{1,30} < 2.55$, $P > 0.1$), suggesting null effects of target faces on ERPs to adaptor faces.

ERPs to Target Faces

Target faces elicited a negative wave at 84–144 ms (N1) and a positive deflection at 148–208 ms (P2) over the frontal–central area, which were followed by a negative wave at 200–300 ms (N2) over the frontal region and a long-latency positivity at 420–580 (P3) over the central/parietal area (Fig. 3). Target faces also elicited a posterior N170 at 140–200 ms over the occipitotemporal area (Fig. 4).

ANOVAs of the N1 amplitudes to target faces did not show any significant effect ($P > 0.1$). ANOVAs of the P2 amplitudes revealed larger amplitudes to other-race than own-race targets ($F_{1,30} > 28.25$, $P < 0.001$). There was a significant effect of Adaptor Expression ($F_{1,30} > 4.38$, $P < 0.05$) due to that targets preceded by pain adaptors elicited smaller P2 amplitudes compared with those preceded by neutral adaptors, demonstrating the presence of RS of P2 amplitudes related to pain expression. This RS effect was further qualified by a significant interaction of Adaptor Expression × Adaptor Race × Target Race ($F_{1,30} > 6.24$, $P < 0.05$). Post hoc analyses confirmed that RS of the P2 amplitude to own-race target faces was significant when the target faces were preceded by own-race adaptors ($F_{1,30} > 7.42$, $P < 0.01$) but "not" when preceded by other-race adaptors ($F_{1,30} < 1.52$, $P > 0.2$, Fig. 3). In contrast, the RS effect on the P2 amplitudes to other-race targets was significant when the target faces were preceded by other-race adaptors ($F_{1,30} > 5.34$, $P < 0.05$) but not when preceded by own-race adaptors ($F_{1,30} < 1$, $P > 0.4$). See Supplementary Table 3 for additional statistic details.

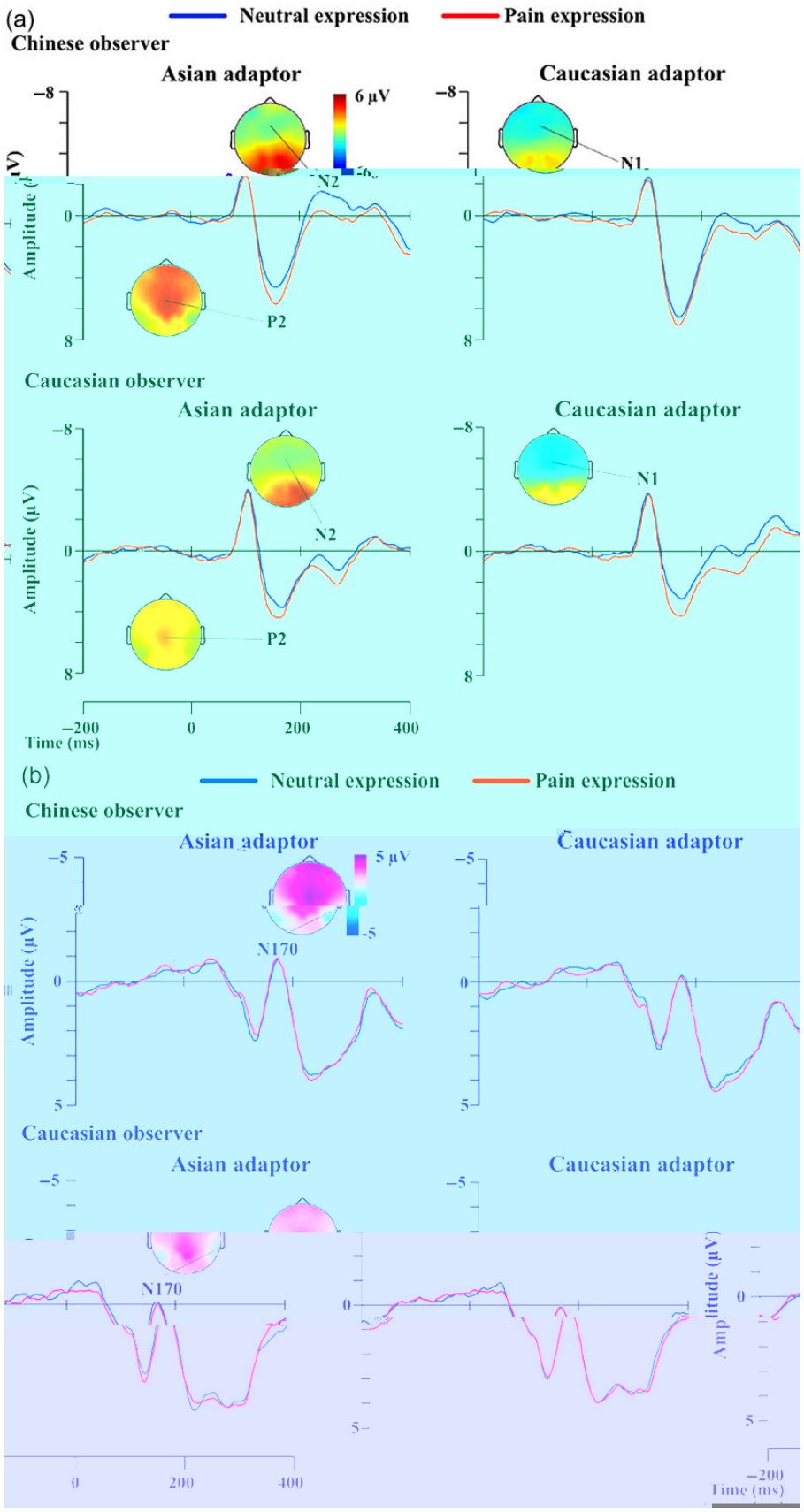

Figure 2. (*a*) Illustration of ERPs to adaptor faces recorded at a central electrode (CZ). Modulations of the P2/N2 amplitudes were stronger when observers perceived racial in-group faces compared with out-group faces. (*b*) Illustration of ERPs to adaptor faces recorded at a right occipitotemporal electrode (P8). There was no evidence for the modulation of N170 amplitude by pain expression. ERPs recorded from Chinese and Caucasian subjects are shown in the upper and lower panels, respectively.

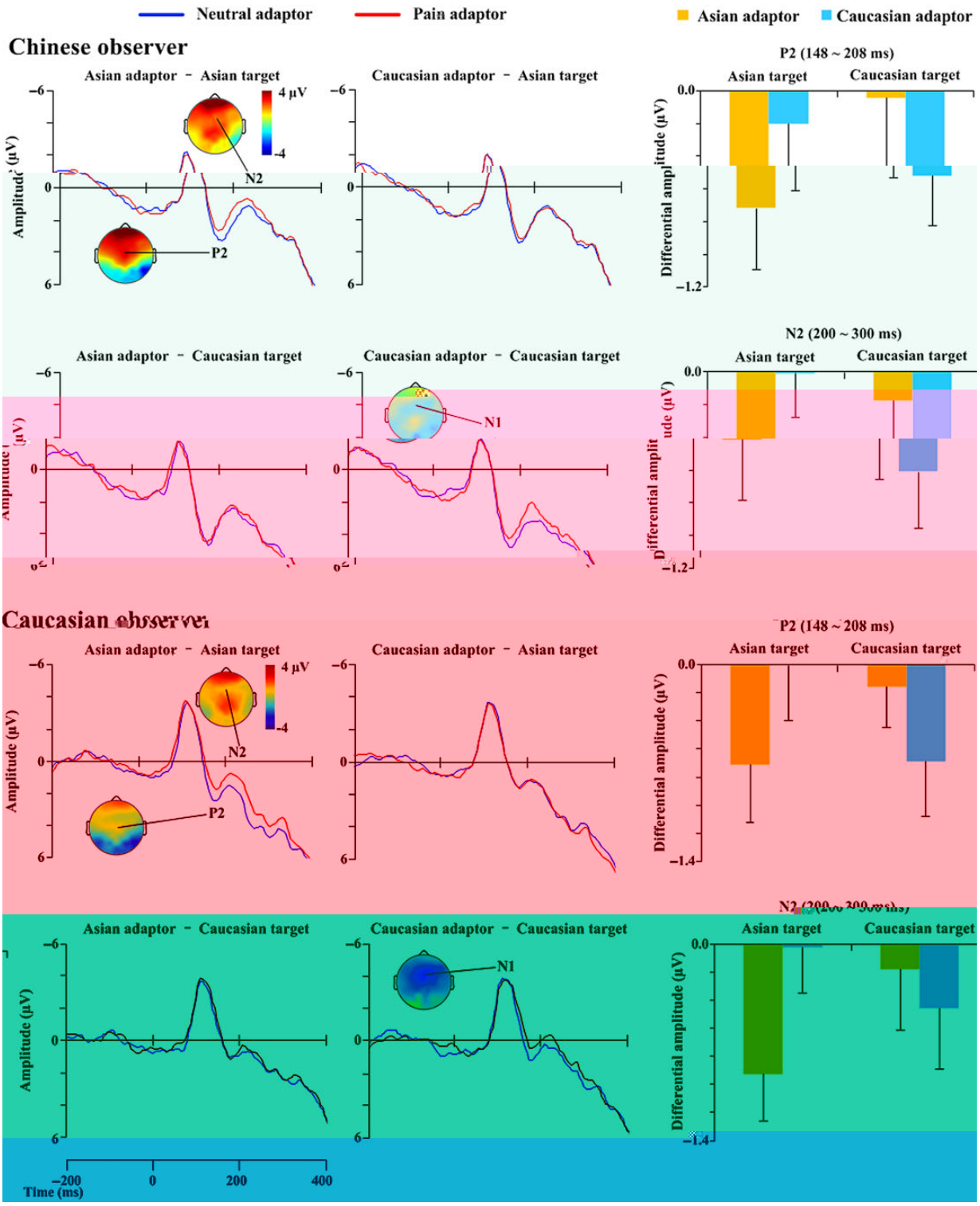

Figure 3. Modulations of pain-related RS of P2 and N2 amplitudes to target faces by social category of adaptor and target faces based on race. ERPs recorded at a CZ to Asian and Caucasian target faces are shown in the left panel. ERPs to target faces preceded by same-race or other-race adaptors are illustrated separately. The bar charts in the right panel show the mean differential amplitudes in the P2/N2 time windows to target faces preceded by pain versus neutral expressions. Overall, pain versus neutral expressions of adaptor faces significantly modulate the P2/N2 amplitudes when adaptor and target faces were of the same race but not when they were of difference races and these effects were similar in Chinese and Caucasian participants.

ANOVAs of the N2 amplitudes showed a significant effect of Target Race ($F_{1,30} > 29.31$, $P < 0.001$), as other-race targets elicited a larger positive shift of the N2 amplitude compared with own-race targets. Moreover, targets preceded by pain versus neutral adaptors elicited smaller positive shift ($F_{1,30} > 4.99$, $P < 0.05$), indicating a pain-related RS effect in the N2 time window. This RS

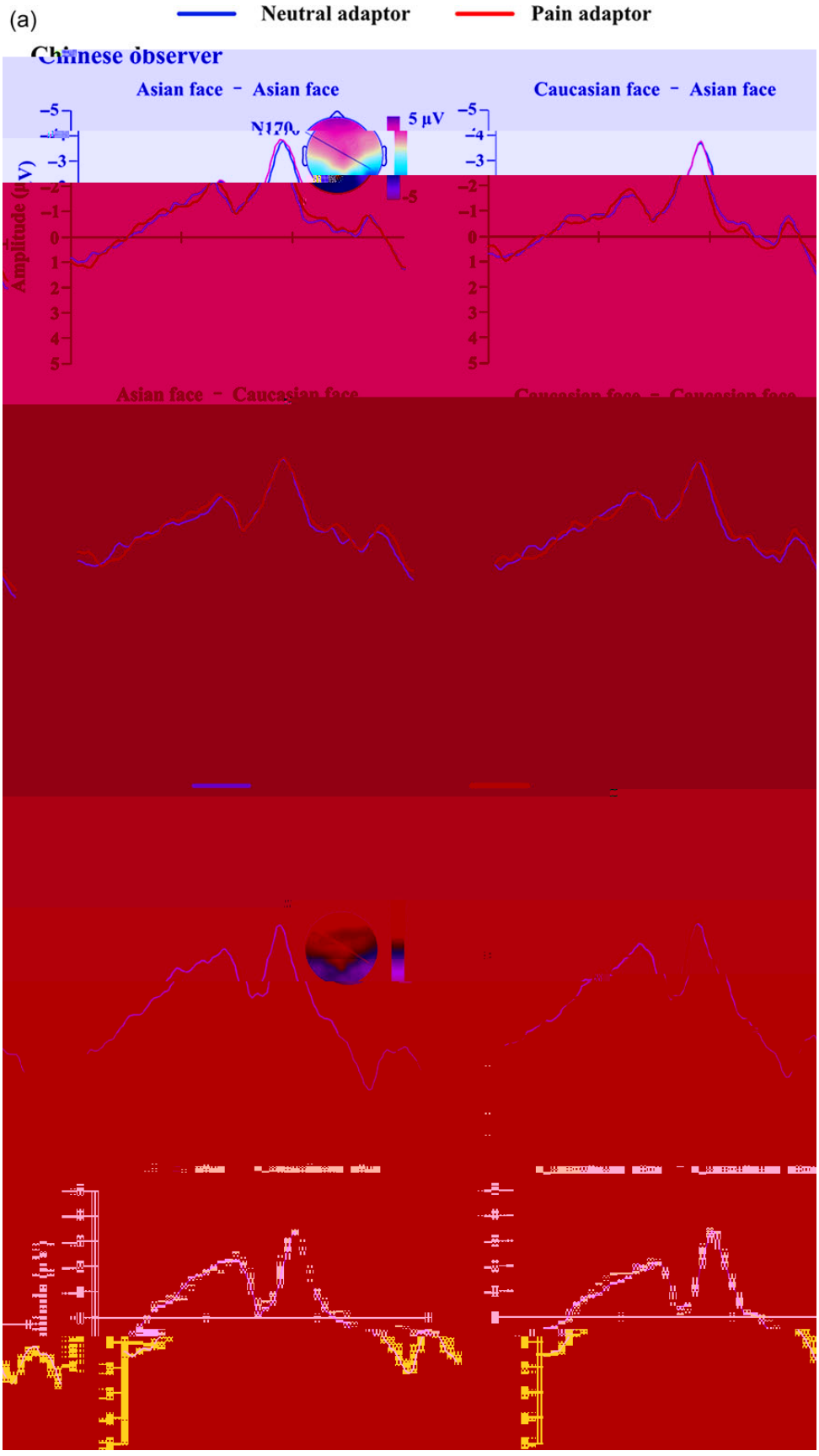

Figure 4. Illustration of the N170 to target faces recorded at a right occipitotemporal eletrode (P8). The N170 amplitude did not show evidence for RS.

effect was also qualified by a significant interaction of Adaptor Expression × Adaptor Race × Target Race ($F_{1,30} > 4.43$, $P < 0.05$). Similarly, the RS effect on the N2 amplitude to own-race targets was marginally significant for own-race adaptors ($F_{1,30} = 2.53$–3.49, $P = 0.071$–0.122) but not for other-race adaptors ($F_{1,30} < 1$, all $P > 0.6$). In contrast, the RS effect on the N2 amplitude to other-race targets was significant for other-race adaptors ($F_{1,30} > 4.65$, $P < 0.05$) but not for own-race adaptors ($F_{1,30} < 1$, $P > 0.4$, Fig. 2). Taken together, the results of the P2 and N2 amplitudes indicate that the pain-related RS occurred when an adaptor and a target were of the same race but not when they were of different races. See Supplementary Table 4 for additional statistic details.

Other-race targets elicited a larger P3 amplitude relative to own-race targets ($F_{1,30} > 15.14$, $P < 0.001$). ANOVAs of the N170 amplitudes also showed a significant effect of Target Race ($F_{1,30} = 10.50$, $P < 0.005$), as own-race targets elicited larger N170 amplitude than other-race targets (Fig. 4). No other significant effect was observed for N170 and P3 amplitudes ($P > 0.05$).

ANOVAs of P2/N2/P3/N170 amplitudes to targets did not show any significant effect of Ethnicity or its interactions with independent variables ($P > 0.05$), suggesting comparable effects of facial expression, intergroup relationships between observers and perceived faces, or RS on ERP amplitudes to target faces in Chinese and Caucasian participants. We also conducted correlation analyses to estimate whether the P2/N2 RS effects were associated with subjective feelings of others' pain and IAT D scores but did not find any significant results ($P > 0.05$).

Pain-Related RS and Intergroup Relationships Determined by Gender

Finally, we examined whether the variation of RS of neural activity to target faces was specific to distinct racial identity of adaptor and target faces. Because there were half female and half male faces used for adaptor and target faces, we tested whether RS of P2/N2 amplitudes to target faces also varied between the conditions when an adaptor and a target were of the same or different genders. We conducted ANOVAs of ERP amplitudes to target faces with Adaptor Gender (own-gender vs. other-gender), Adaptor Expression (pain vs. neutral), Target Gender (own-gender vs. other-gender) as within-subjects variables, and Sex (male vs. female participants) as a between-subjects variables. Own-gender (or other-gender) refers to faces that are of the same gender (or different gender) with participants.

ANOVAs of the N1 amplitudes to target faces did not show any significant effect ($P > 0.1$). ANOVAs of the P2 amplitudes to target faces showed a significant main effect of Adaptor Expression ($F_{1,30} > 11.26$, $P < 0.005$), as target faces preceded by adaptor faces expressing pain elicited smaller P2 amplitudes than did those preceded by neutral expressions (Fig. 5). These results indicated pain-related RS of the P2 amplitude to target faces. However, RS of the P2 amplitude did not differ when adaptor and target faces were of the same gender or different genders ($F_{1,30} < 1$, $P > 0.4$). Similarly, ANOVAs of the N2 amplitudes to target faces revealed a significant main effect of Adaptor Expression ($F1,30 > 14.98$, $P < 0.001$), as target faces preceded by adaptor faces with pain compared with neutral expressions induced a smaller positive shift of the N2 amplitude. However, such modulation of the N2 amplitude did not differ when adaptor and target faces were of the same gender or different genders ($F_{1,30} < 1$, $P > 0.4$). ANOVAs of the P3 and N170 amplitudes to target faces did not reveal any significant effect of Adaptor Expression ($P > 0.05$). Taken together, these results indicate that, while the RS effects on P2 and N2 amplitudes occurred to target faces, whether adaptor and target faces belong to the same social category of gender identity did not affect the pain-related RS of neural activity to target faces. Therefore, the racial identity of adaptor and target faces was the only social factor that led to modulations of the RS effects on P2 and N2 amplitudes to target faces.

Discussion

Although there has been ample evidence for modulations of neural activity by own-race and other-race faces (Ito and Bartholow 2009; Kubota et al. 2012), it remains unknown whether overlapping or distinct neuronal populations are recruited during the processing of emotional states of different races. The current work provides the first electrophysiological evidence for the proposition that, at specific stages of the processing stream, distinct neural assemblies are engaged during the perception of pain expressions of different races. Our data analysis focused on differential ERPs to target faces with pain expressions preceded by adaptor faces with pain versus neutral expressions, which denote a type of RS of neural activity that was independent of perceptual features and person identity of adaptor/target faces but related to their painful emotional states.

We found that, for both Chinese and Caucasian participants, the neural activity to adaptor faces in the P2/N2 time windows over the frontal/central areas was positively shifted by pain expression and this effect was stronger for own-race than other-race faces. These results replicate the previous ERP findings of racial in-group bias in neural responses to perceived pain in others (Sheng and Han 2012; Sheng et al. 2013; Sessa et al. 2014). Most importantly, the pain-related RS of neural activity to target faces in the P2/N2 time windows occurred when adaptor and target faces on each trial were of the same race but not when their racial identities differed. Participants' performances during gender judgments were compatible when an adaptor and a target were of the same race or different races. Thus, the variation of pain-related RS as a function of distinct racial identity of adaptor and target faces cannot be attributed to differences in attentional engagement or motor responses. Furthermore, we demonstrated that race (in terms of both adaptor and target faces) is the only social category to produce significant effects on the pain-related RS of neural activity to target faces. This excludes the possibility that any dissimilarity in facial features that categorize adaptor and target faces into different social groups can cause variations of pain-related RS of neural activity to target faces.

Although there are different models of mechanisms underlying RS effects on brain activity (Grill-Spector et al. 2006; Gotts et al. 2012), it is commonly accepted that the presence of RS of neural activity indicates that the processing of 2 successive stimuli engages the same or overlapping neuronal population (Grill-Spector et al. 2006). Thus, our findings support the distinct-population hypothesis and suggest that distinct neural assemblies are recruited in the processing of pain expressions of different races in the P2/N2 time windows. Although the results of IAT suggest stronger implicit positive attitude toward own-race faces in Caucasian compared with Chinese participants, both groups showed similar modulations of the pain-related RS by racial identity of adaptor and target faces. As such, the employment of distinct neural substrates, which underlies the processing of painful expressions by other-race individuals, appears to occur independent of the individual's implicit attitude toward racial in-group and out-group members.

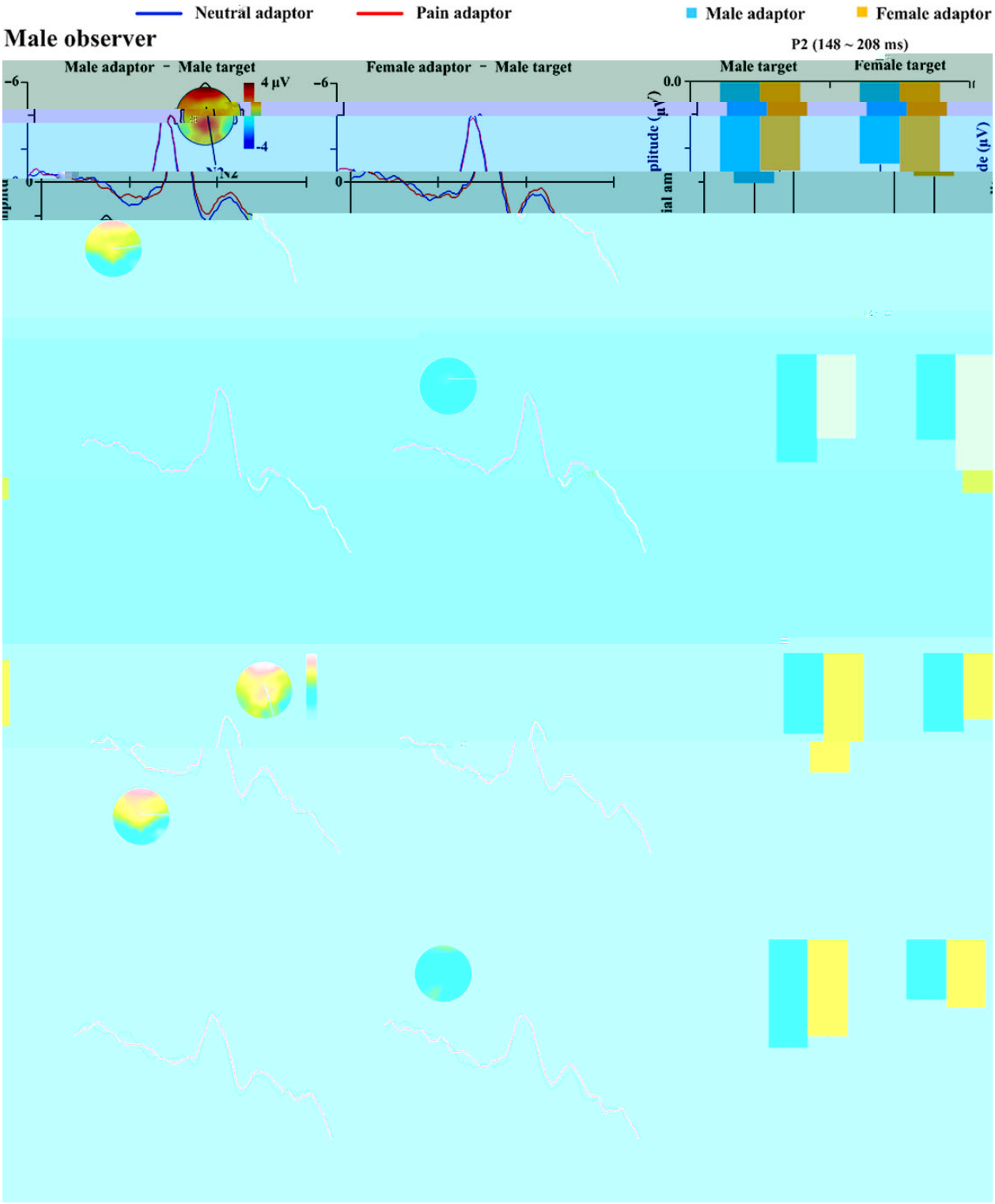

Figure 5. P2/N2 amplitudes to target faces in conditions when adaptor and target faces were of the same gender or of different genders. ERPs recorded at a CZ to target faces (either female or male faces) are shown in the left panel. ERPs to target faces preceded by same-gender or other-gender adaptors with pain neutral expressions are illustrated separately. The bar charts in the right panel show the mean differential amplitudes in the P2/N2 time windows to target faces preceded by pain versus neutral expressions. Overall, pain versus neutral expressions of adaptor faces modulated the P2/N2 amplitudes, but these effects did not differ regardless when adaptor and target faces were of the same gender or of different genders.

Source estimation of the neural activity in the P2 time window that differentiated between pain and neutral expressions suggests an origin in the anterior cingulate cortex (Sheng and Han 2012). This is consistent with the fMRI findings of increased activity in the anterior cingulate cortex and supplementary motor area to pain versus neutral expressions (Saarela et al. 2007;

Sheng et al. 2014) and greater neural activities in these brain areas in response to perceived pain in own-race and other-race individuals (Xu et al. 2009; Azevedo et al. 2013; Sheng et al. 2014). Source estimation of the P2 to adaptor faces in the current study did not produce robust outcomes possibly due to the low signal-to-noise ratio of P2 to adaptor faces. However, the voltage topographies revealed frontal/central distribution of the P2 component in responses to adaptor faces with pain expressions. Similar voltage topographies were observed for the P2 component to by target faces. Future fMRI research should clarify whether perception of own-race and other-race pain activates distinct neuronal populations in the anterior cingulate cortex.

Previous research has uncovered multiple mechanisms underlying stronger neural responses to perceived pain in own-race than in other-race individuals. It has been suggested that the lack of individuated perceptual processing of other-race faces (Valentine and Endo 1992; Vizioli et al. 2010) leads to decreased neural responses to other-race versus own-race pain expressions (Sheng and Han 2012). Recent research also reported that intranasal self-administration of oxytocin increased the P2 amplitude to own-race pain expression but produced little effect on the neural activity related to other-race pain expression (Sheng et al. 2013). These findings suggest that distinct cognitive strategies and distinct neurotransmitters are utilized during the perception of own-race and other-race pain. The findings of the current study further suggest that distinct neuronal populations may be engaged in coding pain expressions of own-race and other-race individuals.

Multiple ERP components such as the frontal/central N1, P2, N2, and the parietal P3 are sensitive to racial identity, particularly to Black and White faces (Ito and Bartholow 2009; Kubota et al. 2012). Modulations of the P2/N2 amplitudes have been interpreted as both early attention orientation to racial out-group faces and deeper levels of attention to familiar racial in-group faces (Ito and Bartholow 2009). Similarly, our previous (Sheng and Han 2012) and current work observed enlarged P2 amplitudes to other-race than own-race faces in Chinese participants. However, the pain-related RS was evident only in the frontal/central P2 and N2 amplitudes. The increased N1 amplitude to other-race compared with own-race faces (e.g., Ito and Urland 2003; Dickter and Bartholow 2007) may reflect early attentional deployment to other-race faces with high novelty, whereas increased P300 amplitudes to individuals who differ in race from preceding individuals (Ito and Urland 2005; Willadsen-Jensen and Ito 2006) are thought to reflect contextual updates along inherently motivationally relevant dimensions (Ito and Bartholow 2009). The posterior N170 has been shown to be sensitive to identity of own-race faces but not that of other-race faces (Vizioli et al. 2010). Our finding that the modulation of pain-related RS of neural activity due to racial identity of adaptor and target faces occurred only in the P2/N2 time windows suggests that distinct neural representations of own-race and other-race pain exist only at a particular stage during face perception.

How do distinct neuronal populations emerge during the perception of own-race and other-race pain? From an ontogenetic perspective, perceptual experiences from a very early stage in life determine what information a neuronal population encodes. Behavioral studies have shown that Caucasian newborn infants do not exhibit spontaneous preference for own-race and other-race faces before 3 months (Kelly et al. 2005). Behavioral impairment in recognizing other-race faces emerges by 6 months of age (Kelly et al. 2007). Adults of Korean origin but adopted by European Caucasian families at the ages of 3 to 9 years perform better at identifying Caucasian faces compared with Asian faces (Sangrigoli et al. 2005). These behavioral findings suggest that the neural system for the recognition of own-race and other-race faces remains plastic during childhood. Distinct neuronal populations engaged in coding own-race and other-race pain may emerge during development when encountering other-race individuals. A neuronal population coding own-race pain expression may emerge at early ages, as in most cases, infants have experiences with own-race parents during early development, whereas a different neuronal population may be engaged in coding other-race pain expression at a later stage of development. This neural model of development of neuronal function of coding own-race and other-race pain is consistent with recent findings that, while humans who had been blind from birth performed as well as healthy individuals in discrimination between faces and houses after recovery of sights by surgery, their N170 did not differentiate between faces and houses (Röder et al. 2013). Therefore, similar performances in discrimination of facial structure or emotional state of faces may be mediated by distinct neural assemblies in the human brain.

From an evolutionary perspective, own-race and other-race pain expressions have different implications for one's own survival. As community conflict is often generated by an influx of new racial or ethnic groups (Oliver and Wong 2003) who are typically regarded as threats by local residents (Ross 2000), perceived pain expression from racial out-group members may signal a potential danger or conflict, whereas pain expression of racial in-group members may be perceived as a signal for help and trigger altruistic behavior to benefit the interest of one's own group. To this end, evolving distinct neuronal populations for coding own-race and other-race pain expressions is propitious to understand the social significance of others' painful feelings so as to make quick decisions during social interactions.

Our findings of RS of neural activity to pain expression of 2 successive same-race faces are not exempt from alternative explanations other than locally based neuronal fatigue. Animal studies have shown evidence for the adaptation of the frontal activity induced by visual stimuli (Verhoef et al. 2008; Mayo and Sommer 2008). fMRI research of humans further revealed modulations of functional connectivity between 2 brain regions by repetition of stimuli with same identity. For example, Ewbank et al. (2011) first found evidence for RS of activity in the extrastriate body area (EBA) and the fusiform body area (FBA) in response to identical images of the same body that varied in body size or view. Moreover, repetition of identical body images induced changes of both forward and backward connectivity between EBA and FBA. These findings suggest that decreased activity in a local region may be attributable to repetition-induced top-down connectivity between 2 brain regions. However, repetition-induced top-down connectivity between 2 brain regions is not necessary in the model that assumes 2 distinct neural modules for coding own-race and other-race pain expressions (own-race pain module and other-race pain module), respectively. According to this model, 2 successive faces with pain expressions, if being of the same race, activate the same module and cause neuronal fatigue. However, an own-race pain expression followed by an other-race pain expression (or in a reverse order) activates 2 different neural modules and thus does not elicit neuronal fatigue of any neural module. On the other hand, the repetition-induced top-down connectivity between 2 brain regions may play a key role in the model that assumes that 2 neural modules are equally employed during the processing of own-race and other-race faces with pain expressions. In this model, the pain module codes painful emotional states of each face independently of its racial identity and the race module codes the racial identity of each face and discriminates racial identity of 2

successive faces. In order to explain our ERP findings, this model assumes inhibitory feedback from the race module to the pain module when 2 successive pain expressions are of the same race but not when they are of different races. The key difference between the 2 models is whether or not the processing of own-race and other-race pain expressions shares the same neural underpinnings, though both models can explain RS of neural activity in response to 2 successive same-race (but not different race) faces with pain expression. Nevertheless, the first model can easily explain racial in-group bias in neural responses to pain expression (e.g., increased P2 amplitudes to own-race than other-race pain expressions of adaptor faces) by assuming a larger neural population for own-race than other-race pain expressions. In contrast, to account for the racial in-group bias in neural responses to pain expression of adaptor faces, the second model must assume additional distinct neural substrates for the processing of own-race and other-race pain expressions at some stage of the processing stream. This would then make the 2 models not be essentially different in terms of distinct/shared neural substrates underlying the processing of own-race and other-race pain expressions. Relative to the second model, the first model proposes more simple mechanisms to explain a number of occurrences, including the RS of neural activity in response to pain expressions of 2 successive same-race faces, the absence of RS of neural activity in response to pain expressions of 2 successive faces of different races, and the racial in-group bias in neural responses to pain expression of adaptor faces.

One limitation of our study is that our fractional factorial design only used target faces with pain expressions. A full factorial design in which Chinese and Caucasian target faces with either neutral or pain expressions follow Chinese and Caucasian adaptor faces with either neutral or pain expressions was not used in our design because such a design would take too long to allow within-subjects EEG recording. The lack of neutral targets does not allow us to compare RS of neural activity related to neutral and pain expressions. Recent ERP and fMRI studies have revealed evidence for attenuated adaptation to emotional expressions (e.g., fear) compared with neutral expressions in the visual cortex (Rotshtein et al. 2001; Schupp et al. 2006; Suzuki et al. 2011; Gerlicher et al. 2014). The ERP component over the occipital-temporal cortex (e.g., N170) in response to pain expressions did not show RS effect in our study. Thus, it is unclear whether pain expression, similar to fear expression, resulted in attenuated adaptation in the occipital-temporal activity. This issue should be addressed in future research.

In conclusion, our ERP results provide evidence for variations of RS of neural activity to pain expressions as a function of the distinct racial identity of adaptor and target faces. Our findings suggest that coding own-race and other-race pain expressions may engage distinct neuronal populations over the frontal regions in specific time windows during the processing stream of faces. Future research should seek to relate our findings of distinct neural representations of own-race and other-race pain expression both to racial in-group bias in empathy for pain (Xu et al. 2009; Avenanti et al. 2010; Sheng and Han 2012; Azevedo et al. 2013; Sheng et al. 2014; Sessa et al. 2014) and to parochial altruism toward racial in-group individuals (Johnson et al. 2002; Drwecki et al. 2011). Our findings also raise a general question for research of emotion, namely, whether comparable findings (i.e., RS of neural activity in response to 2 successive same-race but not different-race faces) exist for other emotional facial expressions. Research along this line can clarify whether overlapping or distinct neuronal populations are engaged in coding basic facial expressions (e.g., fear and happy) of same-race and different-race faces.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

Funding

This work was supported by the National Natural Science Foundation of China (Projects 31470986, 31421003, 91332125 and 81161120539) and the Ministry of Education of China (Project 20130001110049).

Notes

Conflict of Interest: None declared.

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